



Distribution and biological characteristics of Atlantic salmon (*Salmo salar*) at Greenland based on the analysis of historical tag recoveries

David G. Reddin^{1*}, Lars Petter Hansen², Vegar Bakkestuen^{2,3}, Ian Russell⁴, Jonathan White⁵, E. C. E. (Ted) Potter⁴, J. Brian Dempson¹, Timothy F. Sheehan⁶, Niall Ó Maoiléidigh⁵, Gordon W. Smith⁷, Arni Isaksson⁸, Jan Arge Jacobsen⁹, Mark Fowler¹⁰, Kjell Arne Mork¹¹, and Peter Amiro¹²

¹Fisheries and Oceans Canada, PO Box 5667, St John's, NL, Canada A1C5X1

²NINA, Gaustadalleen 21, Oslo N-0349, Norway

³Natural History Museum, University of Oslo, Oslo N-0318, Norway

⁴Cefas, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

⁵Fisheries Science Services, Marine Institute, Rinville, Oranmore, Co. Galway, Ireland

⁶NOAA Fisheries Service, 166 Water Street, Woods Hole, MA 02543, USA

⁷Marine Scotland Science, Inchbraoch House, South Quay, Ferryden DD10 9SL Montrose, Angus, UK

⁸Directorate of Fisheries, Dalshraun 1, 220 Hafnarfjörður, IS-112 Reykjavík, Iceland

⁹Faroe Marine Research Institute, PO Box 3051, Nóatún 1, FO-110 Tórshavn, Faroe Islands

¹⁰Bedford Institute of Oceanography, 1 Challenger Drive, Dartmouth, NS, Canada B2Y 4A2

¹¹Institute of Marine Research, PO Box 1870 Nordnes, Bergen N-5024, Norway

¹²PO Box 925, Chester, NS, Canada B0J1J0

*Corresponding author: tel: +1 709 8952009; e-mail: redding@hotmail.com

Reddin, D. G., Hansen, L. P., Bakkestuen, V., Russell, I., White, J., Potter, E. C. E., Dempson, J. B., Sheehan, T. F., Ó Maoiléidigh, N., Smith, G. W., Isaksson, A., Jacobsen, J. A., Fowler, M., Mork, K. A., and Amiro, P. 2012. Distribution and biological characteristics of Atlantic salmon (*Salmo salar*) at Greenland based on the analysis of historical tag recoveries. – ICES Journal of Marine Science, 69: 1589–1597.

Received 17 August 2011; accepted 18 January 2012; advance access publication 13 June 2012.

In this study, we examined 5481 records of tag recoveries at Greenland from a new tagging database held by ICES that contains information on salmon tagged in Canada, France, Faroes, Greenland, Iceland, Ireland, Norway, Spain, the UK (Northern Ireland, Scotland, England, and Wales), and the United States from the early 1960s to the present. For 4806 of the tag recoveries, latitude and longitude information were available, describing, to varying degrees of accuracy, the location of recovery of tagged fish. Release and recovery dates were variable, but no significant differences over time were noted. The information derived from tag recoveries was used to describe the distribution and growth of salmon of different origins. The proportion of recoveries from East Greenland suggested that potential multi-sea-winter salmon from northern Europe have a more easterly distribution than those from southern Europe. The location of recovery of salmon of North American origin differed from that of European salmon along the west coast of Greenland. Tag recoveries by country were not uniformly distributed across the respective NAFO Divisions. Tags from salmon originating in Canada and the United States were more commonly recovered in northern locations than tags from European-origin salmon. Analysis of rates of tag recovery suggested similar rates before and after the introduction of the NASCO Tag Return Incentive Scheme. The straight-line migration speed of both North American and European salmon changed very little over the time-series, but was ~40% greater for North American salmon (0.43 m s^{-1}) than for European salmon ($0.29\text{--}0.32 \text{ m s}^{-1}$).

Keywords: Atlantic salmon, distribution, Greenland, swim speed, tag recoveries.

Introduction

The life history of the Atlantic salmon (*Salmo salar*) is complex; in general terms, smolts leave their natal rivers in spring, earlier in the south than in the north, and move quickly from coastal waters to the open sea. Recovery of various types of tags applied to salmon showed that they were distributed widely in the North Atlantic (Parrish and Horsted, 1980; Hansen and Quinn, 1998; Holm et al., 2004) with fish spending 1–3, and occasionally up to 5, years feeding at sea before returning to their natal river to spawn (Mills, 1989).

The abundance of wild Atlantic salmon has declined in many parts of their native range as a result of various factors, including losses of habitat attributable to industrial development and urbanization, overfishing, episodic outbreaks of disease and parasites, predation, and changing ocean conditions (Parrish et al., 1998; Jonsson and Jonsson, 2004). Marine survival indices in the North Atlantic have declined and remain low, and factors other than marine fisheries contribute to the continued low abundance of wild Atlantic salmon (ICES, 2011). Systematic efforts including tagging studies have been undertaken to gather data on salmon and especially post-smolts at sea (Lear, 1976; Reddin, 1985; Reddin and Short, 1991; Holst et al., 1993; Shelton et al., 1997; Holm et al., 2000, Anon., 2010; Sheehan et al., 2011). In particular, there is a need to understand better the distribution and migration patterns of salmon at sea, both in time and space, and how this affects survival.

Salmon were reported from the coastal waters of West Greenland as early as 1935, from bycatches in groundfish gear (Jensen, 1939). Directed exploitation of salmon is thought to have begun around 1959 when local fishers set fixed gillnets within fjords and in and around rocks and islets along the coast (Parrish and Horsted, 1980). By the mid-1960s, a summer/autumn fishery pursued by Greenlanders existed along the west coast of Greenland, with a much smaller fishery sporadically taking place near Angmagssalik on the east coast. In 1965, Faroese and Norwegian fishers introduced offshore fishing (usually within 40 nautical miles of the coast) with drift gillnets that were not anchored or set fast to shore. Together with the set gillnets fished closer to shore, the driftnet fishery expanded quite rapidly. The combined catch in both components of the fishery reached ~1300 t by the late 1960s, eventually peaking at ~2700 t in 1971 (ICES, 2011).

Concern was expressed by the main Atlantic salmon-producing countries when tags applied to salmon in rivers around the North Atlantic were first returned from the Greenland fishery in the early 1960s (Parrish and Horsted, 1980), and this fishery was considered to be one of the reasons for lower returns to freshwater (Jensen, 1990). Subsequent studies based on tag recoveries showed that the salmon caught were exclusively multi-sea-winter (MSW) or potential MSW salmon originating in rivers in both Europe and North America (Parrish and Horsted, 1980; Idler et al., 1981). Hence, the rational management of the fishery could only be achieved through international cooperation. Initially, this international forum was provided by the International Commission for the Northwest Atlantic Fisheries (ICNAF), and its agreements included the establishment of a quota of 1190 t per annum for Greenlandic vessels and a phasing-out by 1975 of all salmon fishing by non-Greenlandic vessels. Since 1984, the North Atlantic Salmon Conservation Organization (NASCO) has provided an intergovernmental forum for cooperation on the

conservation, restoration, enhancement, and rational management of wild Atlantic salmon. Through various NASCO agreements, quotas and landings in the West Greenland fishery have been considerably reduced (Colligan et al., 2008), and since 2002, the fishery at West Greenland has been restricted to an internal-use only fishery with annual landings <50 t at West Greenland. Landings at East Greenland in recent years have been 2 t or less. Through international programmes coordinated by NASCO, landings at West Greenland have been regularly sampled for scales, measurements, and other biological metrics (ICES, 2011). In 1989, NASCO introduced a Tag Return Incentive Scheme (NASCO, 1989) in an effort to enhance tag recoveries and to raise awareness of its work. Analysis of historical tag data recovered at Greenland could add significantly to the knowledge base of the distribution and ocean migration of Atlantic salmon and potentially be very useful for managing the resource.

As part of the SALSEA programme developed by NASCO's International Atlantic Salmon Research Board, historical tagging and recovery information for salmon tagged as parr, smolts, or adults in countries around the North Atlantic (referred to below as homewaters) and recaptured at Greenland was compiled into a new database, the Northwest Atlantic Salmon Tagging Database (NASTDE; ICES, 2007, 2008, 2009). This database was analysed to examine patterns and changes in the distribution of salmon originating from both sides of the North Atlantic caught along the coasts of East and West Greenland. Other biological information associated with the tagging database, specifically the tagging and recovery dates, fork lengths, and whole weights of salmon were used to determine differences in swim speeds and size between North American and European salmon.

Methods

Recoveries of external and internal tags from salmon tagged as parr or smolts in homewaters between the 1960s and the 2000s, and from an Icelandic research cruise at East Greenland in 1985 (Thorsteinsson and Gudjonsson, 1986) were used in this paper. A small number of tag recoveries from international tagging experiments at Greenland in the early 1970s (Parrish and Horsted, 1980) were also collated. However, those relate to recoveries in homewaters and at West Greenland from adult fish tagged in the Greenland fishery and have not been examined further here. Most of the recoveries (~98%) were from the commercial salmon fishery operating along the west coast of Greenland, but a few tags were recovered from a small subsistence fishery and/or from scientific surveys that took place intermittently on the east coast. The sources of tagging data and the data themselves are fully described in ICES (2007, 2008, 2009).

NASTDE contains 5481 records of tag recoveries, for which 4806 have latitude and longitude coordinates for the recovery locations. However, because many of the recoveries were made before global positioning satellites were commonly used or were derived from market-based sampling programmes, most of the recovery sites were ascribed latitudes and longitudes for the locations of the communities in Greenland where the salmon were landed. Often, only the NAFO Division was available, and recovery latitudes and longitudes were set to the midpoint of the division area (Figure 1). The dividing line between West and East Greenland was based on the longitude of Cape Farewell, Greenland.

There are several issues with the use of the overall database that are more fully described in ICES (2008). First, the distribution of

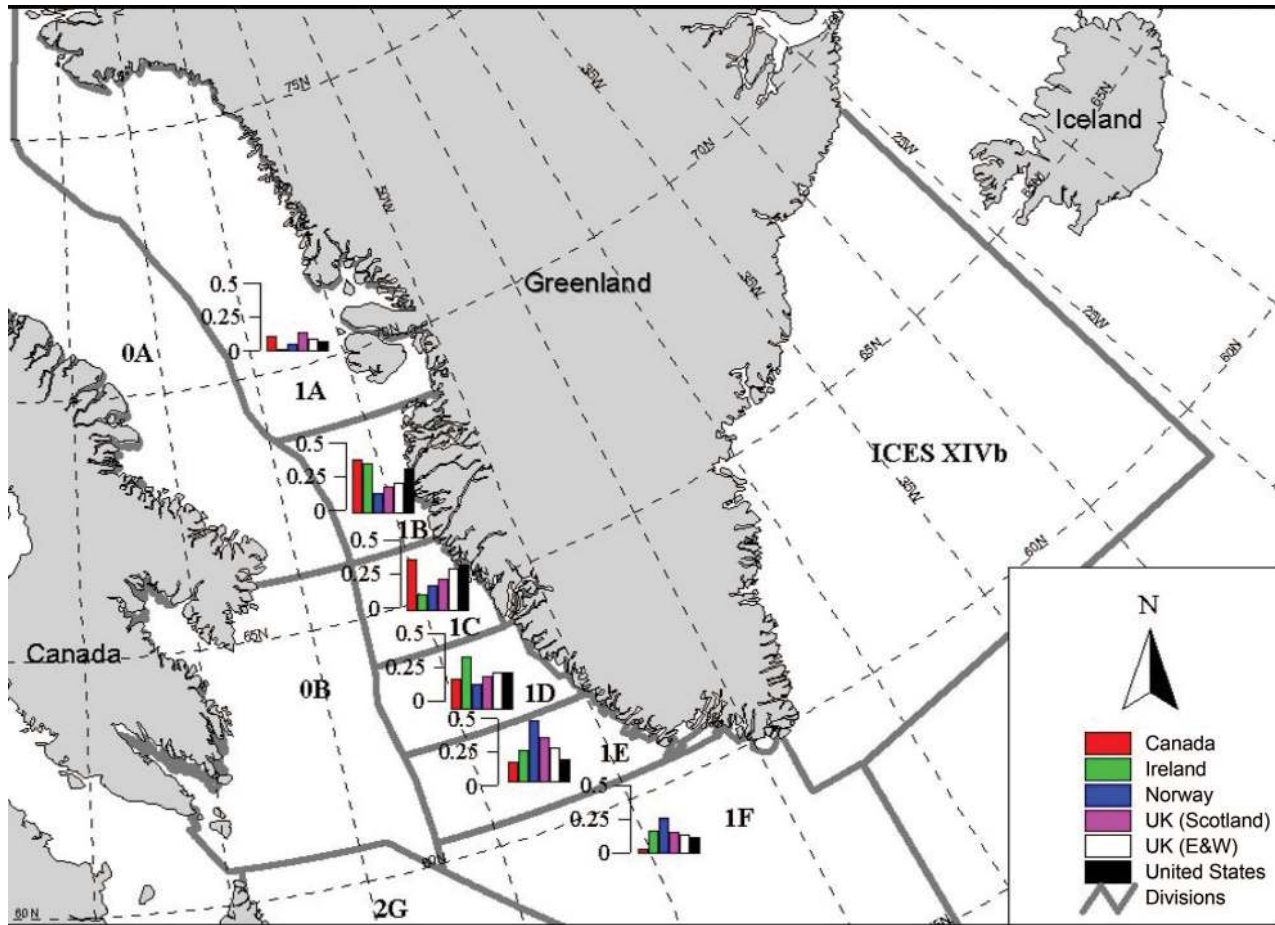


Figure 1. Map showing NAFO Divisions at West Greenland, ICES Statistical Area XIVb, on the east coast of Greenland, and the relative contributions of tag recoveries by country of origin.

tag recoveries depends on the distribution of the fishing effort, which is unknown for the Greenland fishery. Hence, it is not known whether the number of tags recovered from each NAFO Division represents the true distribution of fish, the distribution of fishing effort, or the reliability with which the tags were reported, or a combination of all these. Significantly, in areas and times with no fishing effort, there will be no tag recoveries, although salmon may have been present. Second, the number of tags recovered has not been adjusted either for the number of fish tagged or for the relative production of salmon in each country. Furthermore, most fish were tagged as smolts in homewaters, although smaller numbers were tagged as parr or adults (post-spawning adults in homewaters). Along with the lack of location-specific recovery information for some tags, these factors have limited the analyses to broad general comparisons.

Observational summaries presented as GIS maps were used to provide overviews of the general patterns of distribution and migration of salmon in the Greenland area. Release and recovery dates were examined for temporal trends, which could confound the interpretation of these data. Multiple regressions were also performed to evaluate whether gutted weight or fork length had changed over time. These variables were regressed against recovery year, days at large, release day, and recovery day for fish of both European and North American origin. These analyses, and those related to swim speed, were restricted to the cohort of salmon

that had spent just one winter at sea (1SW) and excluded the relatively small numbers of MSW salmon and previous spawners.

G-tests were used to test for differences in the distribution of tag recoveries and proportions in selected geographic areas. The proportion in each response variable category is hypothesized to be the same for each of the treatment groups. Rates of tag recovery per unit of catch at Greenland before and after the NASCO Tag Return Incentive Scheme were compared by ANOVA. The numbers of US-tagged and -released juvenile salmon were obtained from US sources. Catch information was obtained from ICES (2011). χ^2 and G-tests were programmed in Statistical Analysis Systems software (SAS, 1988) and multiple regressions were performed in R (R Development Core Team, 2011). ArcView was used for the GIS analyses.

Results

Analysis of historical tag data

The time-series of tag recovery information covers a period of 50 years, during which there have been changes to the fishing seasons and quotas and in the timing and intensity of the salmon-tagging programmes. An important assumption in the analyses that follow is whether releases and recoveries are consistent over time. These changes are reflected in the release and recovery dates of salmon of European and North American origin (Figure 2a and b,

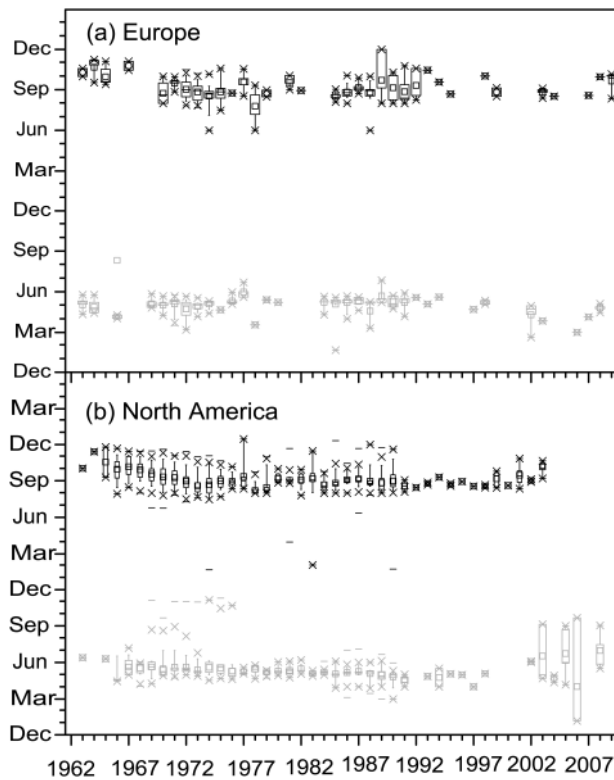


Figure 2. The release (grey) and recovery (black) dates for tagged salmon of (a) European, and (b) North American origin. Each box is the 75th and 25th percentiles, the cross is the data range, median dates are the black horizontal lines, and the black vertical lines are 99th percentiles.

respectively); release dates do not necessarily reflect the smolt emigration date.

For European-origin salmon, release dates ranged from March to June, with 95th percentiles generally overlapping over the 50 years (Figure 2a). Tag recoveries occurred later in the year during the 1960s (between September and November) than for the rest of the time series. Recoveries from the 1970s on were generally in September, but ranged from June to November (95th percentiles). There was a notable reduction in the numbers of salmon tagged and tags recovered in the late 1970s to mid-1980s and from the mid-1990s to 2010. Although release and recovery dates did vary, among-year variations were not notably different from within-year variations, except releases in the 2000s compared with the 1970s, 1980s, and 1990s (ANOVA comparing decadal release days, $F_{4,351} = 10.398$, $p < 0.0001$, and *post hoc* LSD test) and recovery dates of the 1960s (ANOVA, $F_{4,351} = 22.568$, $p < 0.0001$, and *post hoc* LSD test).

Release dates for North American salmon were more varied than for European salmon owing to the tagging and release of kelts and parr (pre-smolts) and tended to be between April and August (Figure 2b). During the early 1970s, there was a large range in release dates, with releases recorded as late as November. In the first half of the 1980s, releases were mainly in May and June, ranging more widely (March–July) in the early 1990s, when numbers of recovered tagged fish declined markedly. From the mid-2000s, when low recoveries were recorded at Greenland, release dates were from April to September. Generally, median release dates from 1970 to 2000 were between

March and April, with comparable inter-95th percentile ranges overlapping. Statistical comparison using ANOVA of decadal release dates did show significant differences ($F_{4,3209} = 82.249$, $p < 0.0001$), with almost all decades significantly differing from each other (*post hoc* LSD test). Recovery dates also showed a broad range across the years 1966–1991, at which time catches declined (ICES, 2011). Inter-95th percentile ranges overlapped among years, but ANOVA of recovery day by decade indicated significant differences ($F_{4,3209} = 67.505$, $p < 0.0001$), with most decades differing from each other.

Basic to the information on the distribution of salmon at sea is whether or not the distributions of recoveries are independent of sea age, i.e. are grilse and MSW or potential MSW salmon found in similar locations? For the Greenland area, the distribution is very dependent on sea age, because only MSW or potential MSW salmon have been caught there (Idler *et al.*, 1981). The salmon fishery at Greenland does not commence until August, and maturing 1SW salmon have already entered or are returning to their home rivers by that time.

Information from tag recoveries (external tags and coded-wire tags) at Greenland over the entire time series were examined to determine whether their distribution was equal among three different regions: northwest Greenland (NAFO Divisions 1A–1C), southwest Greenland (NAFO Divisions 1D–1F), and East Greenland (ICES Statistical Area XIVb). Results for salmon originating in Canada, the United States, Norway, the UK (Scotland), and the UK (England and Wales) were consistent in that tag recoveries for all countries were not uniformly distributed (all χ^2 -tests, $p < 0.0001$). However, because these results are likely to be partly related to the differential distribution of fishing effort among these regions (there is very little salmon fishing at East Greenland), further analysis of the data was carried out for West Greenland to test if tag recoveries were uniformly distributed among the NAFO Divisions. This analysis demonstrated that, for all countries of origin, recoveries were not uniformly distributed across the respective NAFO Divisions (all χ^2 -tests, $p < 0.0001$). Tagged salmon from Canada and the United States were more commonly captured in northern locations (NAFO Divisions 1B and 1C) than European-origin salmon that tended to be caught farther south in NAFO Divisions 1E and 1F. The tag recovery location for salmon of North American origin differed significantly from that of European salmon at West Greenland (likelihood ratio G-test = 1044.88, $p < 0.0001$). Collectively, 35% of North American tag recoveries were in NAFO Divisions 1A and 1B compared with only 23% of European tag recoveries. In contrast, 39% of the tag recoveries from European-origin salmon were from NAFO Areas 1E and 1F compared with only 18% of North American tag recoveries (Figure 1). To investigate whether these differences were caused by differential catch rates between NAFO Divisions and over time, tag recoveries from different countries made in each year and in each NAFO Division were divided by the respective catches in the fishery. The mean results for each country for the years when recoveries were made (as a proxy for years following releases in homewaters; Table 1) showed the same patterns of distribution, with recovery rates (tags per tonne) being higher towards the north for salmon from North America (US and Canadian Maritimes) and higher towards the south for salmon from Europe [UK (Scotland) and UK (England and Wales)].

Within North America, the distribution of Canadian and US tag recoveries at West Greenland also differed (likelihood ratio

Table 1. Mean number of tags from selected countries/regions recovered per tonne of salmon landed in each NAFO Division at Greenland, for years when recoveries were made between 1973 and 2008.

Country of tagging	Mean number per NAFO Division of recapture						
	1A	1B	1C	1D	1E	1F	All divisions
UK (Scotland)	0.005	0.020	0.006	0.005	0.042	0.010	0.026
Canada (Maritimes)	0.091	0.123	0.081	0.047	0.029	0.001	0.059
United States	0.031	0.137	0.143	0.113	0.037	0.030	0.086
UK (England and Wales)	0.002	0.008	0.004	0.007	0.007	0.012	0.011

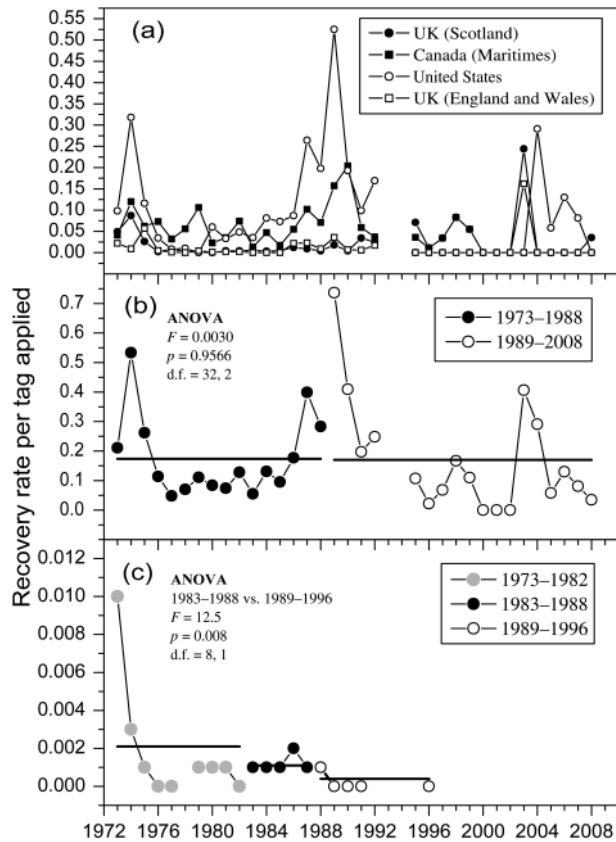


Figure 3. (a) Annual recovery rate adjusted for catch at West Greenland by country of origin and year of recovery. (b) Total recovery adjusted for catch at West Greenland for the periods 1973–1988 (dots) and 1989–2008 (open circles), with respective means (straight lines). (c) The recovery rate of US-tagged salmon from Greenland per tagged fish for the periods 1973–1982 (grey circles), 1983–1987 (dots), and 1988–1996 (open circles). The US Carlin tagging programme ended in 1996, and no tags were applied from 1992 to 1995.

G -test = 81.61, $p < 0.0001$). Tags from Canadian salmon were recovered at a higher rate in more northerly locations than tags from US-origin fish. A comparison of European salmon from Norway, Ireland, the UK (Scotland), and the UK (England and Wales) also indicated differences (likelihood ratio G -test = 53.51, $p < 0.0001$), with tags from Norway and the UK (Scotland) recovered at a higher rate in more southerly areas than those from Ireland and the UK (England and Wales; Figure 1).

Analysis of the rate of recovery of tags (tags per tonne of salmon caught) before and after the NASCO Tag Return Incentive Scheme was introduced in 1989 indicated that there were 0.173 and 0.170

tags recovered per tonne of salmon caught for the periods 1973–1988 and 1989–2008, respectively. These rates were similar when compared by ANOVA ($F = 0.003$, $p = 0.957$). Although initially some additional tags caught at Greenland in earlier years were returned by fishers following the introduction of the Tag Return Incentive Scheme, this analysis suggests that the reward scheme had no apparent influence on the rates of tag recovery (Figure 3b). Recoveries at Greenland of tags that had been applied to juvenile salmon in the United States indicated that the recovery rate per tag applied declined significantly between 1983–1988 and 1989–1996 (Figure 3c), also suggesting that the reward scheme had no apparent influence on tag recoveries at Greenland.

Of all the tag recoveries at Greenland with assigned locations, 4682 (98.7%) were recovered at West Greenland and only 59 (1.3%) at East Greenland. This is consistent with relatively low fishing effort and harvests at East Greenland. The total reported catch of salmon over the period 1960–2007 was 37 382 and 61 t at West Greenland and East Greenland, respectively (ICES, 2011). However, the ratio of tag recoveries to reported catch was much higher for East Greenland (0.97) than for West Greenland (0.125). The tag recoveries at East Greenland were made on an intermittent basis between 1970 and 2009, with a period of above-average recoveries in the mid-1980s (Figure 4).

As noted above, there is a great deal of variability in the distribution of tag recoveries by country of origin at both West and East Greenland (Table 2, Figure 4). The proportional distribution of recoveries was significantly different between countries (χ^2 -test, $p < 0.01$). The proportion of tags recovered at East Greenland was particularly low for fish originating from Ireland and Canada. Of note is the relatively higher rate of recovery of US-origin fish compared with Canadian fish, which suggests a more easterly distribution (East Greenland–Irminger Sea) for the former. In contrast, the proportion of tag recoveries at East Greenland was well above average for Norwegian and Icelandic fish, although the sample size for Icelandic fish was very small. European-origin MSW salmon exploited at West Greenland mainly originated from southern Europe. The large proportion of Norwegian fish at East Greenland relative to the smaller proportion at West Greenland suggests that MSW salmon from northern Europe also have a more easterly distribution than those from southern Europe.

Biological characteristics of recovered tagged salmon

The mean fork length of European salmon at capture declined significantly over the period (Figure 5a; 72.9 cm in 1961 to 61.7 cm in 2009), whereas for North American salmon the mean length at capture significantly increased (Figure 5b; 61.1 cm in 1969 to 68.1 cm in 2007). Multiple regression of the fork length of European salmon against year of recapture, days between release

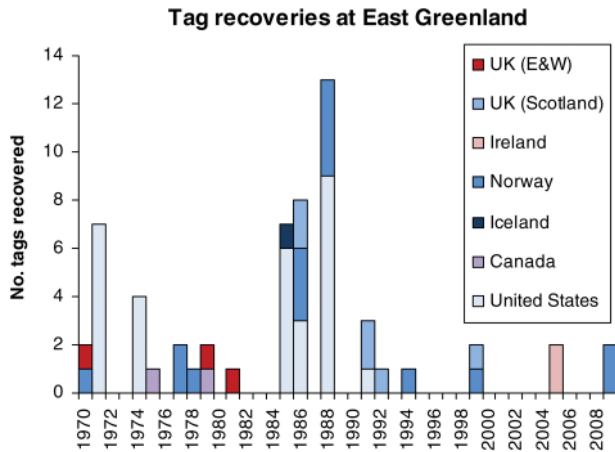


Figure 4. Tags recovered at East Greenland (ICES Statistical Area XIVb) by country of origin and year of recovery.

Table 2. Numbers of tags recovered at Greenland for which location (NAFO Division) was specified, by country of origin, and the percentage of all recoveries for each country reported from East Greenland.

Country	% of recoveries at East Greenland		
	West Greenland	East Greenland	Total
United States	2 128	30	2 158
Canada	1 814	2	1 816
Iceland	16	1	17
Norway	115	15	130
Ireland	139	2	141
UK (Scotland)	273	6	279
UK (England and Wales)	195	3	198
UK (Northern Ireland)	2	0	2
Total	4 682	59	4 741

and recapture, and day of the year of release and recapture showed that fork length declined over the recapture years 1961–2009 (very strong significance of regression on year: $t = -4.35$, $p = 2.67 \times 10^{-5}$; $F = 11.25$ on 4 and 127 d.f., $p = 7.66 \times 10^{-8}$). Multiple regression of the fork length of North American salmon against year of recapture, days between release and recapture, and day of the year of release and recapture showed that the fork length increased over the recapture years from 1969 to 2007 (very strong significance of regression on year: $t = -4.694$, $p = 3.96 \times 10^{-6}$; $F = 9.749$ on 4 and 327 d.f., $p = 1.84 \times 10^{-7}$).

Year was, therefore, a highly significant ($p < 0.001$) driver for both European and North American fork lengths, whereas no other variable was significant in any of the models. Multiple regression of gutted weight of European and North American salmon against year of recapture, days between release and recapture, and day of the year of release and recapture showed that whereas gutted weight appeared to decline over the period 1961–2009 (recapture years), the regressions were not significant.

From the NASTDE, swim speed was calculated from the latitude and longitude of release and the general recovery locations and dates. Distances were calculated as direct paths and travel time is indicative to the day. Regression of swim speed against

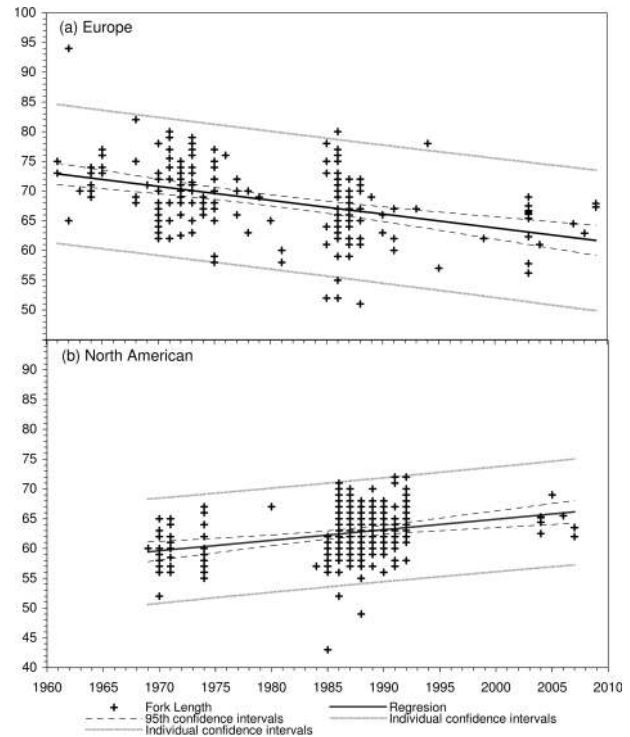


Figure 5. Lengths of tagged salmon of (a) European ($n = 152$) and (b) North American ($n = 154$) origin recovered at Greenland between 1960 and 2010 (analyses are confined to potential MSW salmon that had spent just 1SW). The regression line is the solid black line, the 95th percentiles for regression are the dashed lines, and the 95th percentiles for individual values are the dotted lines.

time showed no statistically significant changes in swim speed ($p > 0.05$). Changes in release and recovery dates over the 50 years may have influenced the calculated swim speeds; however, these tend to have similar averages. Mean swim speeds appear to have decreased very slightly for European-origin 1SW salmon, from 0.32 m s^{-1} in 1961 to 0.29 m s^{-1} in 2009 ($n = 356$; Figure 6a), with no change for salmon of North American origin (0.43 m s^{-1} in 1967 and 2007, $n = 1401$; Figure 6b).

Discussion

This study is based on the compilation of data on the recovery of tagged salmon in Greenlandic waters over a period of almost 50 years. Analysis of historical data on tag recoveries for Greenland adds to the knowledge base on the distribution and ocean migration of Atlantic salmon. Salmon tagged in all countries around the North Atlantic have been recovered in Greenland waters, but very few North American fish have been recaptured farther east and very few European salmon farther west. Reddin *et al.* (1984) were the first to provide information on the migration of salmon from Europe to North America and the reverse. Although overall numbers of tag recoveries were rather low (< 12 from either side of the Atlantic), this represented the first evidence of salmon ranging beyond their previously known migration pathways. Hansen and Jacobsen (2003) conducted a simulation based on tag returns which suggested that Canadian-origin salmon made up 6% of the overall population exploited in the

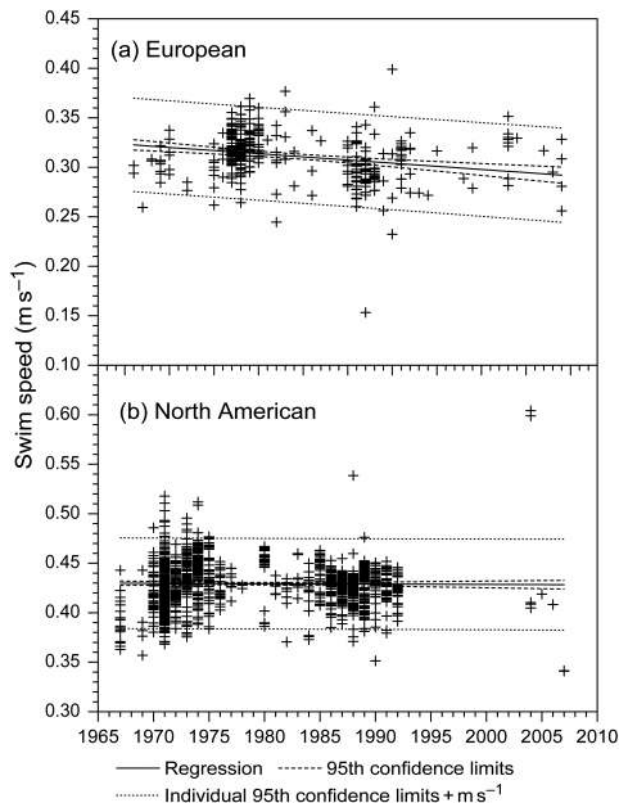


Figure 6. Swim speeds of tagged 1SW salmon (potential MSW) of (a) European ($n = 356$) and (b) North American ($n = 1401$) origin recovered at Greenland between 1960 and 2010 (analyses are confined to potential MSW salmon that had spent just 1SW). The plus symbols are swim speeds (m s^{-1}), the solid lines are the regressions, the dotted lines depict individual 95th percentile confidence limits, and the dashed lines depict regression 95th percentile confidence limits.

Faroese salmon fishery. Based on Caesium-137 (^{137}Cs) levels in salmon returning to the St Marguerite River in Quebec and from patterns of ^{137}Cs in the ocean, Tucker *et al.* (1999) showed that 43% of 1SW and MSW salmon sampled had levels consistent with having spent time east of Iceland around the Faroe Islands, and in the Norwegian, North, and Irish Seas. Using a similar technique, Spares *et al.* (2007) and Dadswell *et al.* (2010) estimated that 25% of 1SW salmon returning to Canada had spent time east of the Faroe Islands. The high values detected by Tucker *et al.* (1999) and Dadswell *et al.* (2010) are in sharp contrast to the generally held view, and the evidence from recaptures of tagged fish, that intercontinental migrations of salmon are rather infrequent. The results of Tucker *et al.* (1999) for 1SW salmon were especially surprising in that they would require the fish to have travelled across the Atlantic and back in 12–14 months. Overall, the number of salmon tagged in North America recaptured east of Greenland has been very low compared with the millions of smolts tagged and does not support the conclusions from the ^{137}Cs studies. Moreover, biomagnifications of radionuclides are known in some fish and marine mammals (Gray, 2002) and, if occurring in Atlantic salmon, would call into question the findings based on the ^{137}Cs studies.

Greenlandic waters are, therefore, the only area where North American and European salmon concentrate extensively together.

However, this study has shown that for all countries of origin, salmon tag recoveries were not uniformly distributed across NAFO Divisions at West and East Greenland. First, a greater proportion of recaptures of US-origin salmon than of Canadian-origin salmon and salmon from northern Europe compared with southern Europe was made at East Greenland. For example, the proportion of recaptures at Greenland of tagged salmon originating from Norway and Iceland (0.109) made in the east was six times that for tagged salmon originating from Ireland and the UK (0.018). Moreover, at West Greenland, tagged salmon from Canada and the United States were more commonly captured in northern locations, whereas tagged European salmon tended to be caught farther south. This mirrors estimates of the proportion of North American and European salmon in the catches at West Greenland from 1969 to the present based on the analysis of scale characteristics and genotyping (ICES, 2011) and confirms the high variability in the relative proportions among both years and latitude (based on NAFO Divisions). There are probably several reasons for these variable distributions, including freshwater conditions in the home river and varying oceanographic conditions either at Greenland or along the route taken by salmon to get to Greenland. Varying fishing patterns along the coast from one year to the next could also mask the true distributions. Nevertheless, we conclude that the distribution of salmon of various origins differs from north to south along the West Greenland coast.

More-detailed information on the latitude and longitude of tag recovery and fishing effort data could allow for more sophisticated analyses similar to those undertaken for ocean distributions of other anadromous fish, including Arctic charr (Dempson and Kristofferson, 1987), brown trout (Kallio-Nyberg *et al.*, 2002), and Atlantic salmon (Juttila *et al.*, 2003). Inherent in the interpretation of these results, or any subsequent analyses that may be undertaken, is the recognition that tag recoveries are derived from fisheries, and so are dependent on the distribution of fishing effort. However, analyses of these data are important, because they can be informative of relative patterns across time between stocks in the areas sampled. In the absence of information on the actual numbers of tags released from different areas, it is not possible to scale the recoveries relative to a common denominator. Ideally, tag recoveries should be scaled to the numbers of fish tagged as well as to the number caught or preferably to the catch per unit effort.

The mean fork length of European salmon recaptured at Greenland decreased between the 1960s and 2000s, whereas the mean length of North American salmon increased. Mean weight did not change for either European or North American salmon during this period. Our analyses suggest that these findings are not related to changes in release or recovery dates, which have remained similar over the study period, i.e. the number of days the salmon have spent at large since being tagged has not changed. A similar analysis was conducted by ICES (2011) using a shorter time-series of data obtained from the structured catch sampling programme of the West Greenland fishery. This showed no clear trends in the predicted whole weight of 1SW non-maturing salmon from North America and Europe, adjusted to a common fork length of 64 cm and a standard sampling week (week 36) between 2002 and 2010. However, the time-series of tag recoveries is considerably longer, and the recoveries are derived from the whole fishery, whereas the sampling programme is restricted in both time and space. Therefore, although the

assumptions inherent in these two approaches were different, the results are consistent. Further analysis should be pursued because stock-specific changes in biological characteristics could provide further insights into the mechanisms behind the differential rates of a decline in different stock groupings across the Atlantic. Changes in condition could have negative consequences for growth, reproduction, and survival of Atlantic salmon populations (Schaffer and Elson, 1975; Friedland *et al.*, 1993). These factors also need to be considered in forecast models for the management of distant-water and homewater fisheries.

The straight-line migration speed of both North American and European salmon changed very little over the time-series, but was ~40% greater for North American salmon (0.43 m s^{-1}) than for European fish ($0.29\text{--}0.32 \text{ m s}^{-1}$). Although this may reflect differences in the swimming speeds of the two groups, this appears unlikely because the salmon are of similar size. Furthermore, there is no evidence from the tag recoveries that North American salmon arrive at West Greenland before European fish. It is, therefore, most likely that European fish take a less direct route to Greenland. This is consistent with current knowledge about the movement of post-smolts from Europe, which appear to begin their marine migration by swimming north into the Norwegian Sea during their first summer at sea, rather than west towards Greenland (Holm *et al.*, 2004).

In 1989, NASCO introduced a tag reward scheme with the goal of increasing recoveries of tags in all fisheries for salmon including the fishery at Greenland. The first rewards were applied to tagged salmon caught in 1988. Our analysis of the rates of tag recovery per tonne harvested at Greenland indicated that the scheme may not have increased tag recoveries. It might be noted, however, that the tag reward scheme is for external tags only, and the majority of tags recovered at Greenland since the 1980s have been CWTs. For the US tagging programme, the recovery rate for salmon tagged as juveniles did not increase in the years following introduction of the NASCO Return Incentive Scheme, and in fact declined. The results would be more conclusive also if adjusted for the number of tagged salmon released by other countries, information unavailable to us.

This first-ever analysis of tag-return data from all countries contributing to the Greenland fishery is an important step in understanding the spatial characteristics of the historical Greenland fishery and the distribution of stocks migrating to Greenlandic waters. The programmes undertaken to obtain these data are generally quite expensive, often involving large trapping facilities that need to be operated over extended periods. It is, therefore, important to ensure that the best use is made of the information and that their value is enhanced when recoveries from a number of programmes (i.e. tagging in different locations and at different times) are analysed together. The analyses presented provide researchers with new information to help guide the next steps in understanding the factors driving marine survival of Atlantic salmon. Additionally, knowledge of the distribution of salmon stocks from different countries may be useful for managers in introducing fishing patterns at Greenland that could reduce or eliminate harvests of stocks that are most at risk. For example, there appear to be large numbers of US-origin salmon at East Greenland, and managers could consider controlling exploitation in this area to protect stocks at risk. In this context, it is notable that this fishery is not currently subject to international agreements in NASCO. Country-specific information might assist managers to incorporate risk into their decision-making at a finer scale,

because the fishery is currently being managed according to the individual contributing stock complexes. More importantly, this analysis has shown distributions of salmon originating within various North American and European stock complexes at Greenland and how they have changed over time. The results also support the findings that different stock complexes contribute differentially to the fishery (Gauthier-Ouellet *et al.*, 2009; Sheehan *et al.*, 2010), and they provide further support for the pursuit of the genetic analysis of current and historical samples.

Acknowledgements

We acknowledge all the biologists and technicians who have been involved over the past six decades in collecting, collating, and archiving the data described in this paper. Without their dedicated efforts, there would be no data and therefore no new knowledge to help us understand the ocean dynamics of the Atlantic salmon and to learn how best to manage and protect the stocks. The participation of VB and KAM in the workshops that developed the Northwest Atlantic Salmon Tagging Database was made possible by funding from NASCO's International Atlantic Salmon Research Board.

References

- Anon. 2010. Mid-term report (April 2008–September 2009) of the EU FP7 project 'SALSEA-Merge' (advancing understanding of Atlantic salmon at sea: merging genetics and ecology to resolve stock-specific migration and distribution patterns). Project 212529, EU Commission. 64 pp.
- Colligan, M., Sheehan, T., Pruden, J., and Kocik, J. 2008. The challenges posed by international management of Atlantic salmon: balancing commercial, recreational and societal interests—The North Atlantic Salmon Conservation Organization (NASCO). *In* International Governance of Fisheries Ecosystems: Learning from the Past, Finding Solutions for the Future, pp. 1–22. Ed. by M. G. Schechter, N. J. Leonard, and W. W. Taylor. American Fisheries Society, Bethesda, MD. 458 pp.
- Dadswell, M. J., Spares, A. D., Reader, J. M., and Stokesbury, M. J. W. 2010. The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the 'Merry-Go-Round' hypothesis. *Journal of Fish Biology*, 77: 435–467.
- Dempson, J. B., and Kristofferson, A. H. 1987. Spatial and temporal aspects of the ocean migration of anadromous Arctic char. *American Fisheries Society Symposium*, 1: 340–357.
- Friedland, K. D., Reddin, D. G., and Kocik, J. F. 1993. Marine survival of North American and European salmon: effects of growth and environment. *ICES Journal of Marine Science*, 50: 481–492.
- Gauthier-Ouellet, M., Dionne, M., Caron, F., King, T. L., and Bernatchez, L. 2009. Spatiotemporal dynamics of the Atlantic salmon (*Salmo salar*) Greenland fishery inferred from mixed-stock analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 2040–2051.
- Gray, J. S. 2002. Biomagnification in marine systems: the perspective of an ecologist. *Marine Pollution Bulletin*, 45: 46–52.
- Hansen, L. P., and Jacobsen, J. A. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. *ICES Journal of Marine Science*, 60: 110–119.
- Hansen, L. P., and Quinn, T. P. 1998. The marine phase of Atlantic salmon (*Salmo salar*) life cycle, with comparison to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(Suppl. 1): 104–118.
- Holm, M., Hansen, L. P., Holst, J. C., and Jacobsen, J. A. 2004. Atlantic salmon. *In* The Norwegian Sea Ecosystem, pp. 315–356. Ed. by H. R. Skjoldal. Tapir Academic Press, Trondheim. 559 pp.

- Holm, M., Holst, J. C., and Hansen, L. P. 2000. Spatial and temporal distribution of post-smolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES Journal of Marine Science*, 57: 955–964.
- Holst, J. C., Nilsen, F., Hodneland, K., and Nylund, A. 1993. Observations of the biology and parasites of postsmolt Atlantic salmon, *Salmo salar*, from the Norwegian Sea. *Journal of Fish Biology*, 42: 962–966.
- ICES. 2007. Report of the Workshop on the Development and Use of Historical Salmon Tagging Information from Oceanic Areas. ICES Document CM 2007/DFC: 02. 60 pp.
- ICES. 2008. Report of the Workshop on Salmon Historical Information—New Investigations from Old Tagging Data. ICES Document CM 2008/DFC: 02. 51 pp.
- ICES. 2009. Report of the Workshop on Learning from Salmon Tagging Records. ICES Document CM 2009/DFC: 05. 39 pp.
- ICES. 2011. Report of the Working Group on North Atlantic Salmon. ICES Document CM 2011/ACOM: 09. 286 pp.
- Idler, D. R., Hwang, S. J., Crim, L. W., and Reddin, D. G. 1981. Determination of sexual maturation stages of Atlantic salmon (*Salmo salar*) captured at sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 38: 405–413.
- Jensen, A. S. 1939. Concerning a change of climate during recent decades in the Arctic and Subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and physical changes. *Det Konglige Danske Videnskabernes Selskab Biologiske Medd*, 14: 1–77.
- Jensen, J. M. 1990. Atlantic salmon at Greenland. *Fisheries Research*, 10: 29–52.
- Jonsson, B., and Jonsson, N. 2004. Factors affecting marine production of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 2369–2383.
- Jutila, E., Jokikokko, E., Kallio-Nyberg, I., Saloniemi, I., and Pasanen, P. 2003. Differences in sea migration between wild and reared Atlantic salmon (*Salmo salar* L.) in the Baltic Sea. *Fisheries Research*, 60: 333–343.
- Kallio-Nyberg, I., Saura, A., and Ahlfors, P. 2002. Sea migration pattern of two sea trout (*Salmo trutta*) stocks released into the Gulf of Finland. *Annales Zoologici Fennici*, 39: 221–235.
- Lear, W. H. 1976. Migrating Atlantic salmon (*Salmo salar*) caught by otter trawl on the Newfoundland continental shelf. *Journal of the Fisheries Research Board of Canada*, 33: 1202–1205.
- Mills, D. H. 1989. *Ecology and Management of Atlantic Salmon*. Chapman and Hall, London. 351 pp.
- NASCO. 1989. NASCO Tag Return Incentive Scheme. NASCO Council Document, CNL(89)17. 3 pp.
- Parrish, B. B., and Horsted, S. A. (eds) 1980 ICES/ICNAF Joint Investigation on North Atlantic salmon. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 176. 146 pp.
- Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D., and Reeves, G. H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 51(Suppl. 1): 281–287.
- Reddin, D. G. 1985. Atlantic salmon (*Salmo salar*) on and east of the Grand Bank. *Journal of Northwest Atlantic Fishery Science*, 6: 157–164.
- Reddin, D. G., Shearer, W. M., and Burfitt, R. F. 1984. Inter-continental migrations of Atlantic salmon (*Salmo salar* L.). ICES Document CM 1984/M: 11. 9 pp.
- Reddin, D. G., and Short, P. B. 1991. Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 2–6.
- R Development Core Team. 2011. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. 103 pp.
- SAS. 1988. *SAS Procedures Guide*, Release 6.03 Edition. SAS Institute Inc., Cary, NC, USA. 441 pp.
- Schaffer, W. M., and Elson, P. F. 1975. The adaptive significance of variation in life history among local populations of Atlantic salmon in North America. *Ecology*, 56: 577–590.
- Sheehan, T. F., Legault, C. M., King, T. L., and Spidle, A. P. 2010. Probabilistic-based genetic assignment model: assignments to sub-continent of origin of the West Greenland Atlantic salmon harvest. *ICES Journal of Marine Science*, 67: 537–550.
- Sheehan, T. F., Renkawitz, M. D., and Brown, R. W. 2011. Surface trawl survey for US origin Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, 79: 374–398.
- Shelton, R. G. J., Holst, J. C., Turrell, W. R., MacLean, J. C., McLaren, I. S., and Nicoll, N. T. 1997. Records of post-smolt Atlantic salmon, *Salmo salar* L., in the Faroe–Shetland Channel in June 1996. *Fisheries Research*, 31: 159–162.
- Spares, A. D., Reader, J. W., Stokesbury, M. J. W., McDermott, T., Zikovskiy, L., Avery, T., and Dadswell, M. J. 2007. Inferring marine distribution of Canadian and Irish Atlantic salmon (*Salmo salar* L.) in the North Atlantic Ocean from tissue concentrations of bioaccumulated Caesium-137. *ICES Journal of Marine Science*, 64: 394–404.
- Thorsteinsson, G., and Gudjonsson, Th. 1986. Experimental salmon fishing at East Greenland in summer 1985 and recaptures of tagged fish. ICES Document CM 1986/M: 25. 12 pp.
- Tucker, S., Pazzia, I., Rowan, D., and Rasmussen, J. B. 1999. Detecting pan-Atlantic migration in salmon (*Salmo salar*) using ¹³⁷Cs. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2235–2239.

Handling editor: Emory Anderson